

Differential effects of word length and visual contrast in the fusiform and lingual gyri during reading

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Previous studies have shown differential responses in the fusiform and lingual gyri during reading and suggested that the former is engaged in processing local features of visual stimuli and the latter is engaged in global shape processing. We used positron emission tomography in order to investigate how these regions are modulated by two common variables in reading: word length (three, six and nine letters) and perceptive similarity to the background (high and low contrast). Increasing both word length and visual contrast had a positive monotonic effect on activation in the bilateral fusiform. However, in the lingual gyrus, activation increased with increasing word length but decreased with increasing contrast. On the basis of previous studies, we suggest that (i) increasing word length increases the demands on both local feature and global shape processing, but (ii) increasing visual contrast increases the demands on local feature processing while decreasing the demands on global shape processing.

Keywords: word length; visual contrast; reading; visual cortex; positron emission tomography (PET)

1. INTRODUCTION

This paper is concerned with the variables that modulate activation in the visual cortex during reading. First, we review previous functional imaging studies of reading that report activation in the visual cortex when either the stimulus, its presentation or the task are manipulated. Then we specifically investigate how activation in different regions of the visual cortex is modulated by changing two common variables in reading: the number of letters present (word length) and their perceptive similarity to the background (visual contrast).

As expected from lesion studies in both animals and humans, functional neuroimaging studies have shown that the visual cortex is critical to pattern recognition including reading. For instance, there is extensive activation in both the striate and extrastriate cortices when reading is contrasted with viewing a visual fixation point (Petersen *et al.* 1988; Jernigan *et al.* 1998) or relative to resting with eyes closed (Price *et al.* 1996a; Brunswick *et al.* 1999). Activation is also sensitive to the number of letters and/or visual features presented at a time (Indefrey *et al.* 1997), the rate at which the words are presented (Price *et al.* 1996a) and the duration they remain in the visual field (Price *et al.* 1994, 1996a; Price & Friston 1997). The effect of rate and duration on visual activation distinguishes distinct functional roles for the posterior fusiform and lingual gyri. For instance, in the bilateral posterior fusiform gyrus, activation increases monotonically with the number of words presented or their duration on the screen, whereas in the lingual gyrus, activity decreases with increasing stimulus duration (Price & Friston 1997)

and is unaffected by rate of presentation (Price *et al.* 1996). Moreover, in the fusiform gyrus, but not in the lingual gyrus, activation increases bilaterally with degrading the integrity of letters during word identification and recognition (Jernigan *et al.* 1998); the words were degraded by removing parts of the letters, thereby making them appear fragmented. Overall, these studies indicate that activation in different regions of the visual cortex is differentially modulated by changes in the visual input (see table 1 for details).

Even when the visual input is matched, activation in the visual cortex is sensitive to the visual or cognitive processing demands. This was first demonstrated by Petersen *et al.* (1988) who reported increased activation in the left extrastriate cortex for words and pseudowords (relative to visual fixation), but not for consonant letter strings and false fonts that had equivalent visual complexity. On the basis of the association of pure alexia with lesions to the extrastriate cortex, Petersen *et al.* (1988, 1990) argued that the function of the left extrastriate region corresponded to a word form system. The coordinates of this extrastriate region (see table 1) indicate a left lateralized region in the vicinity of the left calcarine sulcus at the most anterior part of the lingual gyrus.

Other studies have confirmed that the left anterior and medial posterior regions of the left lingual gyrus are sensitive to task demand, even when visual features are controlled (Price *et al.* 1994, 1997; Moore & Price 1999). For example, activation in these regions increases when reading aloud is contrasted with viewing words silently and saying 'okay' (see table 1). Both reading aloud and silently involve activation of the visual word form system, but one might argue that reading aloud places greater demands on the word form system than saying an

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Table 1. Areas and coordinates of regions that showed increased activation in previous studies on reading (The coordinates relative to the studies by Petersen *et al.* (1988, 1990) are reported after being changed from Talairach & Szikla (1967) to Talairach & Tournoux (1988).)

	left fusiform			right fusiform			left/medial lingual			right/medial lingual			
visual input changes													
Petersen <i>et al.</i> (1988)													
reading– fixation	—	—	—	—	—	—	–24	–70	2	26	–78	6	
	—	—	—	—	—	—	–6	–84	10	12	–84	10	
Petersen <i>et al.</i> (1990)													
reading– fixation	—	—	—	—	—	—	–29	–65	2	—	—	—	
	—	—	—	—	—	—	–21	–75	2	—	—	—	
Brunswick <i>et al.</i> (1999)													
reading– rest	–22	–94	–10	29	–98	–8	—	—	—	6	–80	0	
Price <i>et al.</i> (1996)													
reading– rest	–26	–74	–16	20	–86	–12	—	—	—	4	–82	–4	
positive effect of rate	–24	–86	–12	22	–82	–12	—	—	—	—	—	—	
positive effect of duration	–26	–80	–16	24	–84	–16	—	—	—	—	—	—	
Price & Friston (1997)													
positive effect of duration	–29	–98	–8	30	–92	–8	—	—	—	—	—	—	
negative effect of duration	—	—	—	—	—	—	–2	–70	–12	—	—	—	
Bookheimer <i>et al.</i> (1995)													
view objects– control	—	—	—	—	—	—	–18	–76	0	—	—	—	
name objects– control	—	—	—	—	—	—	–22	–78	0	—	—	—	
Jernigan <i>et al.</i> (1998)													
effect of degrading words	–30	–90	–16	36	–78	–12	—	—	—	—	—	—	
visual input is consistent													
Price <i>et al.</i> (1996)													
object naming– viewing	–32	–92	–8	—	—	—	–14	–72	4	—	—	—	
Moore & Price (1999)													
objects and words	—	—	—	—	—	—	–16	–72	–12	—	—	—	
naming– viewing	—	—	—	—	—	—	–8	–68	–8	—	—	—	
Fink <i>et al.</i> (1998)													
global > local attention	—	—	—	—	—	—	—	—	—	16	–74	0	
local > global attention	–22	–96	–8	—	—	—	—	—	—	—	—	—	

irrelevant word irrespective of stimulus. However, the word form explanation has been challenged by a number of different investigators. Howard *et al.* (1992) found no differences in the striate or extrastriate cortex when reading aloud was contrasted with saying ‘crime’ in response to strings of false fonts (although see Price *et al.* 1994). Bookheimer *et al.* (1995) and Moore & Price (1999) found regions with very similar coordinates (see table 1) for object as well as for word processing and found no difference when reading was contrasted with object processing. Indefrey *et al.* (1997) demonstrated that activation changes in the visual cortex were related to the length or visual complexity of the stimulus (although the coordinates of the activations were not reported). Clearly then, activation in the lingual gyrus is not specific to words.

An alternative to the word form hypothesis (Price *et al.* 1997) is that the left medial lingual gyrus is involved in some aspect of visual processing that is modulated when subjects are required to make a stimulus-specific response such as naming. This explanation gains some support from a functional imaging study by Fink *et al.* (1996) that employed the Navon (1977) task. Fink *et al.*’s (1996) study involved the presentation of hierarchically organized letters (global letters composed of local letters) and a requirement to attend to the identity of either the local or

global parts. Activation increased in the right medial posterior lingual gyrus when attention was directed to the global parts and in the left fusiform gyrus when attention was directed to the local parts. Since the visual input remained the same, irrespective of task, Fink *et al.*’s (1996) study suggested that the bilateral fusiform gyrus was concerned with local feature processing and the right medial posterior lingual gyrus was concerned with global shape processing. If these results are applied to those from reading studies (see above), we might deduce that subjects attend more to the global shape of words or objects when a naming response is required (Moore & Price 1999) or when the words are presented for short durations (Price & Friston 1997). If we applied Fink *et al.*’s (1996) results to the finding by Jernigan *et al.* (1998), we might also deduce that subjects attend more to the local features when they read words composed of degraded letters.

In the study we report in the present paper, we investigated how responses in the visual cortex are influenced by changing two common variables, which are used to investigate visual aspects of reading: word length and visual contrast. Previous behavioural results have shown that both increasing word length and decreasing visual contrast prolong naming times (e.g. Frederiksen & Kroll 1976; Weekes 1997; Herdman *et al.* 1999). The task was held constant by requiring subjects to read all words. On

the basis of the results of Indefrey *et al.* (1997), we predicted that increasing the number of letters would increase activation in both the lingual and posterior fusiform gyri: long words should challenge both global and local visual processing more than short words. Our predictions concerning the effect of contrast were less clear because we are unaware of any functional imaging studies that have manipulated visual contrast during reading. Jernigan *et al.* (1998), investigating the effect of degrading the integrity of letters, found an increase in activity in the fusiform gyri for both identifying and recognizing degraded words, possibly due to increased demand in local letter processing. It may be that any variable increasing the difficulty of visual processing will similarly increase the magnitude of local letter processing. The same would then occur with low-contrast words. On the other hand, it can also be argued that low-contrast words will engage global processing selectively. This follows because cells responding to low spatial frequency components in images continue to respond under low-contrast conditions, unlike cells responding to high spatial frequency components (e.g. Livingstone & Hubel 1987). Hence, activation in the lingual gyrus may be greatest for low-contrast words and it may decrease as contrast increases (when more local letter identification processes become engaged).

2. METHODS

Six healthy male subjects with normal or corrected-to-normal vision were presented with 40 serially unrelated words during each scan. The experiment comprised a 3×2 factorial design. The variables were (i) word length (three, six and nine letters) and (ii) visual contrast (low and high contrast). The high-contrast stimuli were white letters on a mid-grey background and the low-contrast stimuli were light-grey letters on a mid-grey background. In the high visual contrast condition there was a clear perceptive contrast between the letters and the background, while in the low visual contrast condition the letters and background were perceptively less distinct. Each word was centred at fixation. Upper-case letters were 11 mm high by *ca.* 4 mm wide and lower-case letters were 8 mm high by *ca.* 4 mm wide and all words were viewed from a distance of 40–60 cm. Words appeared equally often in upper and lower case. Stimulus exposition was 500 ms and the interstimulus interval was 1000 ms. The task was constant across the experimental conditions: subjects were asked to articulate the names of the words silently. Words were matched for frequency and *n* count across word lengths and they were balanced across the high- and low-contrast conditions across subjects.

Twelve positron emission tomography (PET) scans were acquired for each subject (two for each of the six conditions) using a Siemens/CPS Ecat HR+ (962) head scanner (Siemens/CTI, Knoxville, TN, USA) and the data were analysed with Statistical Parametric Mapping (SPM97, Wellcome Department of Cognitive Neurology, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>) implemented in Matlab (Mathworks Inc., Sherbon, MA, USA). Prior to statistical analysis the images for each subject were realigned using the first as a reference in order to correct for any interscan head movements. Realigned images were stereotactically normalized in a standard space of Talairach & Tournoux's (1988) atlas and smoothed in order to account for variations in gyral anatomy and individual

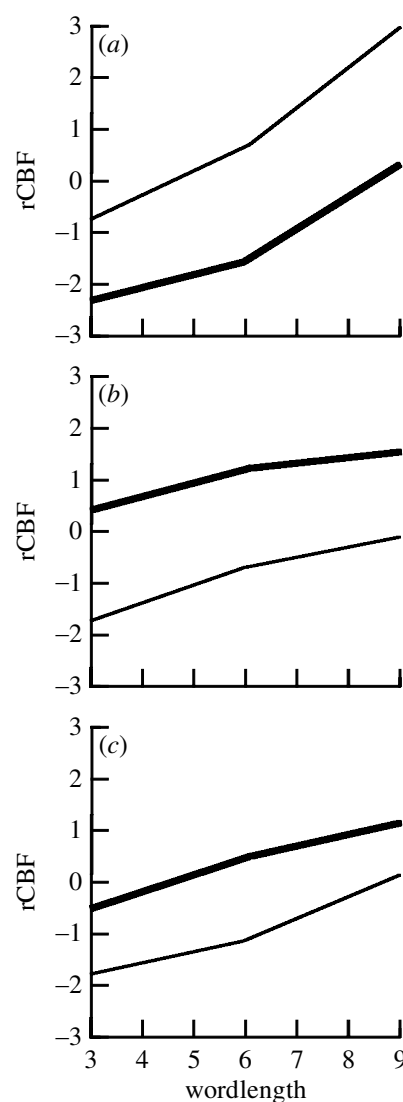


Figure 1. Normalized rCBF in (a) the medial lingual gyrus (4, -76, -4), (b) the right fusiform gyrus (34, -90, -8) and (c) the left fusiform gyrus (-24, -72, -4). The positive monotonic effect of word length was not modulated by visual contrast and vice versa. However, the rCBF response was bigger for low-contrast stimuli (thin line) in the lingual gyrus and for high-contrast stimuli (thick line) in the bilateral fusiform gyri.

variability in functional neuroanatomy and to improve the signal-to-noise ratio (Friston *et al.* 1995). The statistical analysis addressed (i) the effect of word length, (ii) the effect of visual contrast, and (iii) their interaction in the visual cortex. The effect of long relative to short words was addressed by contrasting (i) nine-letter words to three-letter words, (ii) nine-letter words to six-letter words, and (iii) six-letter words to three-letter words. On the other hand, the effect of short relative to long words was addressed by contrasting (i) three-letter words to nine-letter words, (ii) three-letter words to six-letter words, and (iii) six-letter words to nine-letter words. Detected activations were discussed only if significant at corrected ($p < 0.05$) or uncorrected ($p < 0.001$) level. The latter was applied to the visual cortex (occipital regions only) and the former was applied to all other voxels in the brain (where we had no *a priori* predictions).

Table 2. The effect of word length and visual contrast on neural activity in the visual cortex

(The table presents areas, coordinates and Z -scores of the regions that showed increased activation for long relative to short words, for low relative to high visual contrast words and for high relative to low visual contrast words. Z -scores of activations significant at corrected level ($p < 0.05$) are marked with an asterisk.)

	effect of word length long – short				effect of visual contrast low – high				high – low			
	x	y	z	Z -score	x	y	z	Z -score	x	y	z	Z -score
left medial lingual	– 10	– 84	– 6	5.8*	—	—	—	—	—	—	—	—
right superior lingual	4	– 84	2	5.3*	—	—	—	—	—	—	—	—
medial cuneus	0	– 76	8	5.2*	—	—	—	—	—	—	—	—
right medial lingual	4	– 76	– 8	4.3	4	– 76	– 8	3.2	—	—	—	—
left fusiform	– 22	– 82	– 12	3.8	—	—	—	—	– 24	– 82	– 16	3.3
right fusiform	32	– 90	– 8	3.1	—	—	—	—	32	– 90	– 10	3.3

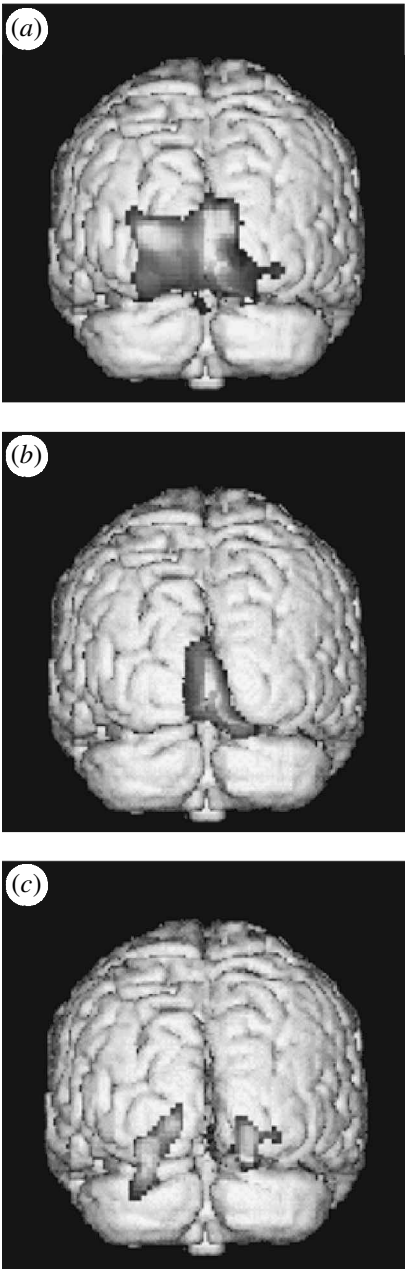


Figure 2. Visual cortex regions where rCBF (a) increased for the reading of long words, (b) increased during the reading of low-contrast words and (c) increased during the reading of high-contrast words.

3. RESULTS

(a) Word length

Relative to short words, long words activated posterior visual areas. In particular, there was an increase in activity bilaterally in the medial lingual (Z -score = 5.8) and fusiform (Z -score = 3.8) gyri, the right superior lingual gyrus (Z -score = 5.3) and the medial cuneus (Z -score = 5.2) (see table 2). Significant activation uncorrected for multiple comparisons was also detected in the left motor region ($x = -58, y = -2, z = 32$ and Z -score = 3.3). When short words were compared with long words, no significant activation was found.

The increased activation in the left motor cortex, which was found for long relative to short words, may be regarded as an effect of a silent subarticulation performed by the subjects. It can be further considered a confirmation that the subjects were articulating the words.

The monotonic positive effect of word length on visual cortex activity for both low- and high-contrast stimuli is shown in figure 1 where normalized regional cerebral blood flow (rCBF) is plotted for both low and high visual contrast stimuli of varying word length. Figure 2 illustrates the location of activations in the fusiform and lingual gyri.

(b) Visual contrast

Low contrast relative to high contrast enhanced activation in the right medial lingual gyrus (Z -score = 3.2). The opposite result occurred in the fusiform gyri; here, high contrast relative to low contrast enhanced activation (Z -score = 3.3) (see table 2).

(c) Interaction

There were no interactions at a corrected level of significance. However, at an uncorrected level ($p < 0.001$ and Z -score of interaction = 3.1), the right middle occipital gyrus ($x = 24, y = -84$ and $z = 26$) was engaged by (i) long relative to short words for high contrast only (Z -score = 3.5), and (ii) low relative to high contrast for short words only (Z -score = 3.4). Looking at the activations plotted for each of the six conditions (three, six and nine letters \times high and low contrast), it was evident that this double effect was mostly due to considerably lowered activation in the three-letters, high-contrast condition.

4. DISCUSSION

The study reported in this paper investigated (i) the effect of word length, (ii) the effect of visual contrast, and (iii) their interaction in the visual cortex during reading.

Word length had a monotonic positive effect on neural activity in both the medial and lateral occipital cortices. This finding is consistent with the increased activation previously found in the lingual and posterior fusiform gyri when the number of components (letters or false fonts) was increased (as in Indefrey *et al.* 1997). However, the effect of visual contrast differentiated the lingual and bilateral fusiform gyri as functionally segregated regions: the lingual gyrus was enhanced by low-contrast words and the fusiform gyri by high-contrast words. The dissociation between the lingual and fusiform gyri fits PET evidence on processing of compound letters when these areas are selectively linked to global and local processing (Fink *et al.* 1996). In our study, word length had a positive effect in both the lingual and bilateral fusiform gyri, consistent with longer words increasing the demands on both local feature and global shape processing. On the other hand, low contrast appeared to decrease the demands on local feature processing while increasing the demands on global shape processing. Fink *et al.*'s (1996) findings also allow us to interpret the apparent discrepancy between the effects of visual contrast and letter degradation as reported by Jernigan *et al.* (1998): our data suggest that, while subjects rely on processing of local features when they read words composed of degraded letters, they attend more to the global shape when they read low-contrast words. Whether this change reflects alterations in visual attention to local and global forms or differences in processing unmodulated by attention is a question awaiting future research.

5. CONCLUSIONS

We found differential responses in the fusiform and lingual gyri to word length and visual contrast in reading. This suggests that (i) the demand on local feature processing increases with varying word length and contrast, and (ii) the demand on global shape processing increases with increasing word length and decreasing contrast.

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REFERENCES

- Bookheimer, S. Y., Zeffiro, T. A., Blaxton, T., Gaillard, W. & Theodore, W. 1995 Regional cerebral blood flow during object naming and word reading. *Hum. Brain Mapp.* **3**, 93–106.
- Brunswick, N., McCrory, E., Price, C. J., Frith, C. D. & Frith, U. 1999 Explicit and implicit processing of words and pseudowords by adult developmental dyslexics. A search for Wernicke's Wortschatz? *Brain* **122**, 1901–1917.
- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J. & Dolan, R. J. 1996 Where in the brain does visual attention select the forest and the trees? *Nature* **382**, 626–628.
- Frederiksen, J. R. & Kroll, J. F. 1976 Spelling and sound: approaches to the internal lexicon. *J. Exp. Psychol. Hum. Percept. Perform.* **2**, 371–379.
- Friston, K. J., Holmes, A., Worsley, K. J., Poline, J. B., Frith, C. D. & Frackowiak, R. S. J. 1995 Statistical parametric maps in functional imaging. A general linear approach. *Hum. Brain Mapp.* **2**, 189–210.
- Herdman, C. M., Chernecki, O. & Norris, D. 1999 Naming cAsE aLtErNAtiVe words. *Mem. Cogn.* **27**, 254–266.
- Howard, D., Patterson, K., Wise, R., Brown, W. D., Friston, K., Weiller, C. & Frackowiak, R. S. J. 1992 The cortical localization of the lexicons: positron emission tomography evidence. *Brain* **115**, 1769–1782.
- Indefrey, P., Kleinschmidt, A., Merboldt, K.-D., Kruger, G., Brown, C., Hagoot, P. & Frahm, J. 1997 Equivalent responses to lexical and nonlexical visual stimuli in occipital cortex: a functional magnetic resonance imaging study. *NeuroImage* **5**, 78–81.
- Jernigan, T. L., Ostergaard, A. L., Law, I., Svarer, C., Gerlach, C. & Paulson, O. 1998 Brain activation during word identification and word recognition. *NeuroImage* **8**, 93–105.
- Livingstone, M. S. & Hubel, D. H. 1987 Psychophysical evidence for separate channels for the perception of form, color, movement and depth. *J. Neurosci.* **7**, 3416–3468.
- Moore, C. J. & Price, C. J. 1999 Three distinct ventral occipito-temporal regions for reading and object naming. *NeuroImage* **10**, 181–192.
- Navon, D. 1977 Forest before trees: the precedence of global features in visual perception. *Cogn. Psychol.* **9**, 353–383.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M. & Raichle, M. E. 1988 Positron emission tomography studies of the cortical anatomy of single-word processing. *Nature* **331**, 585–588.
- Petersen, S. E., Fox, P. T., Snyder, A. Z. & Raichle, M. E. 1990 Activation of extrastriate and frontal cortices areas by words and word-like stimuli. *Science* **249**, 1041–1044.
- Price, C. J. & Friston, K. J. 1997 The temporal dynamics of reading: a PET study. *Proc. R. Soc. Lond. B* **264**, 1785–1791.
- Price, C. J., Wise, R., Watson, J., Patterson, K., Howard, D. & Frackowiak, R. S. J. 1994 Brain activity during reading: the effects of task and exposure duration. *Brain* **117**, 1255–1269.
- Price, C. J., Moore, C. J. & Frackowiak, R. S. J. 1996a The effect of varying stimulus rate and duration on brain activity during reading. *NeuroImage* **3**, 40–52.
- Price, C. J., Wise, R. J. S. & Frackowiak, R. S. J. 1996b Demonstrating the implicit processing of visually presented words and pseudowords. *Cerebr. Cortex* **6**, 62–70.
- Price, C. J., Moore, C. J. & Friston, K. J. 1997 Subtractions, conjunctions, and interactions in experimental design of activation studies. *Hum. Brain Mapp.* **5**, 265–272.
- Talairach, J. & Szikla, G. 1967 *Atlas d'anatomie stéréotaxique du télencéphale*. Paris: Masson & Cie.
- Talairach, J. & Tournoux, P. 1988 *A co-planar stereotactic atlas of the human brain*. Stuttgart, Germany: Thieme.
- Weekes, B. S. 1997 Differential effect of number of letters on word and nonword naming latency. *Q. J. Exp. Psychol.* **A50**, 439–456.